

Part III: Habitats

Chapter 22

Using the past to understand the future: palaeoecology of coral reefs

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*Perhaps the earth is teaching us when everything
seems dead and then everything is alive.*

Pablo Neruda

22.1 Introduction

Present anthropogenically-induced climate change is now well substantiated⁹¹. The effects of climate change on the marine biosphere are the subject of great concern^{64,133,63} but we simply do not have enough long-term ecological data to predict potential changes in the geographic distribution and composition of marine communities. Hence, long-term time-series data on the past response of marine ecosystems to climate change have become increasingly relevant. Coral reefs provide a legacy of their existence because they accumulate vast thicknesses of biogenic sediments, so it is possible to acquire time-series ecological data in the form of variations in reef coral community structure during past episodes of environmental change. It is perhaps fortuitous that many of the proxies that we use to understand past climate on earth can be found in the major architectural components of reefs, the scleractinian corals. However, most emphasis has been placed on using corals as ancient thermometers and much less on their ecological response to global climate change.

22.1.1 Defining history

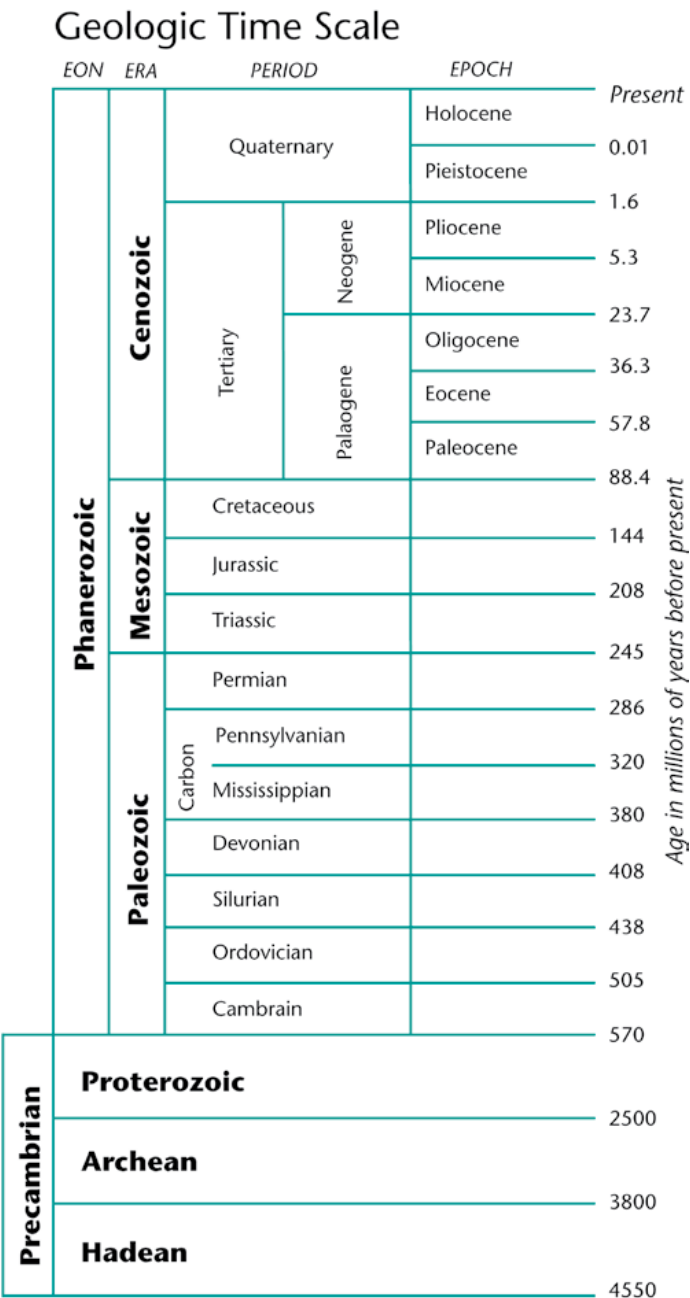
There have been many attempts to place the present and projected global climate change into an historical context (eg Crowley³²). However, most of these attempts are undertaken by palaeoclimatologists interested in the comparisons of rates and magnitudes of physical change, but not the corresponding rates and magnitudes of ecological change. In this contribution we take a close look at the major climatic variables most likely to change in the coming century by tracing their history throughout various intervals of geological time. We conveniently divide these intervals into 'deep time' and the Quaternary (Pleistocene and Holocene; see Figure 22.1) so that lessons can be learned from multiple time scales. After we discuss these physical changes, we summarise the biological response of tropical marine ecosystems, with special attention to coral reefs. We then present a series of examples of the response of coral reefs to past global climate change and use these results to provide guidance as to likely scenarios for the future of the Great Barrier Reef (GBR) under predicted climate change.

This contribution covers a large range of spatial and temporal scales. Throughout, it is critically important to consider the scale-dependence of our discussion. The derivation of principles and analogies from geological timescales and perspectives is often not directly applicable to studies and events occurring at ecological timescales. For example, current concern over the future of the GBR is placed in the context of upcoming decades or centuries. The geological record can be used to examine responses of reef ecosystems to both prolonged and rapid perturbations in the past. However, the resolution to determine how reefs 'looked' during intervals (decades to centuries) over which rapid perturbations occurred is only sporadically encountered (eg Pandolfi et al.¹⁰²).

On the other hand, the unfolding of natural ecological processes often occurs over time spans that are far greater than those directly observable by living scientists. This may leave critical challenges to managers of marine ecosystems over the short time scales inherent in human generations, or even shorter political cycles. The geological record of coral reefs is the exclusive (and hence, indispensable) source of data that can inform managers about processes operating over longer time intervals. In this chapter we attempt to summarise the relationship between past climate and the ecological history of reefs. We find that, in the absence of human impacts, reefs either persisted in the face of natural changes in climate throughout their long geological history, despite large environmental variability, or that any deleterious ecological effects were superseded by replenished ecosystems.



Figure 22.1 Geological time scale^a showing the age of the Phanerozoic (deep time) and the Quaternary



^a US Geological Survey: <http://www2.nature.nps.gov/geology/usgsnps/gtime/gtime1.html>

22.2 Vulnerability of coral reefs to climate change

22.2.1 Exposure

22.2.1.1 Phanerozoic rates and magnitudes of environmental change

Physical controls on reef building and decline, over geologic timescales, include variations in seawater chemistry and cyclic changes (at varying time scales) in sea level, sea surface temperature and global levels of atmospheric CO₂. These factors are necessarily interrelated. In the following sections, we outline the nature and distribution of these factors over the last 540 million years – the Phanerozoic Eon of geologic time (Figure 22.1).

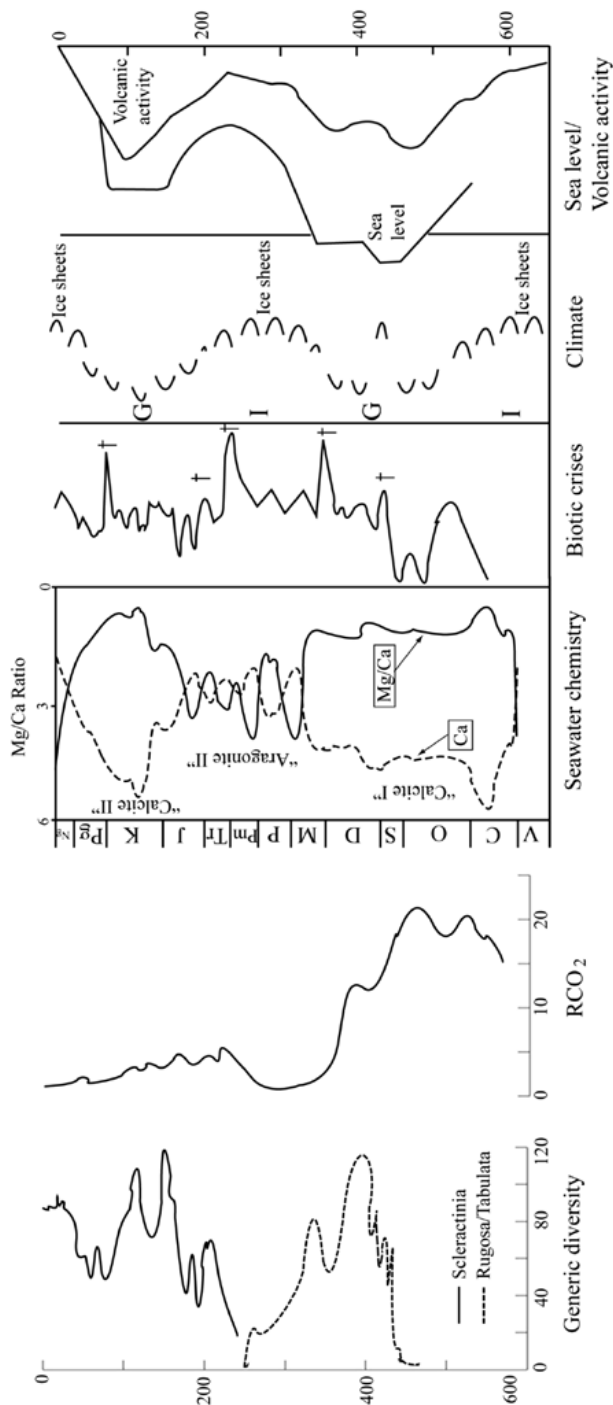
Seawater chemistry

The mineralogy of inorganically precipitated calcium carbonate varied between calcite and aragonite over geologic time¹¹⁴, calcite is the more stable of the two and has typically been better preserved. The Phanerozoic Eon can be divided into three intervals of ‘aragonite seas’ and two intervals of ‘calcite seas’ based on which mineral phase was predominant (Figure 22.2). ‘Aragonite I,’ ‘Calcite I’ and a portion of ‘Aragonite II’ are encompassed by Palaeozoic time (an interval of approximately 300 million years). ‘Calcite II’ occurs from Jurassic–Oligocene time (170 million years), followed by ‘Aragonite III’ which began approximately 30 million years ago and continues today. Wilkinson and Algeo¹³⁹ and Hardie⁵⁶ suggested that each of these intervals is related to secular (extremely long-term) shifts in the magnesium/calcium (Mg/Ca) ratio of sea water imparted by changes in spreading rates along mid-ocean ridges. Stanley and Hardie¹²⁵ expanded this work by relating secular oscillations in the carbonate mineralogy of carbonate-secreting taxa to the intervals of calcite or aragonite precipitation described by Sandberg¹¹⁴. Their work was, in turn, corroborated by Dickson³⁴ who used the mole percent of Mg-rich calcite in skeletal elements of fossil echinoderms as proxy for Mg/Ca ratios in sea water during Aragonite I, II and Calcite I, II.

Values for surface ocean pH and alkalinity have been established for the last 60 million years^{103,104} (Figure 22.3). From a low value of 7.4 at the beginning of Paleogene time (Greenhouse II), sea surface pH increased to a Miocene high of 8.3 before declining to its current level of 8.1 (note no data are available for the Late Eocene and Oligocene epochs). In the context of this time scale, the fact that sea surface pH declined from 8.2 to 8.1 in only the last 40 years is particularly sobering.

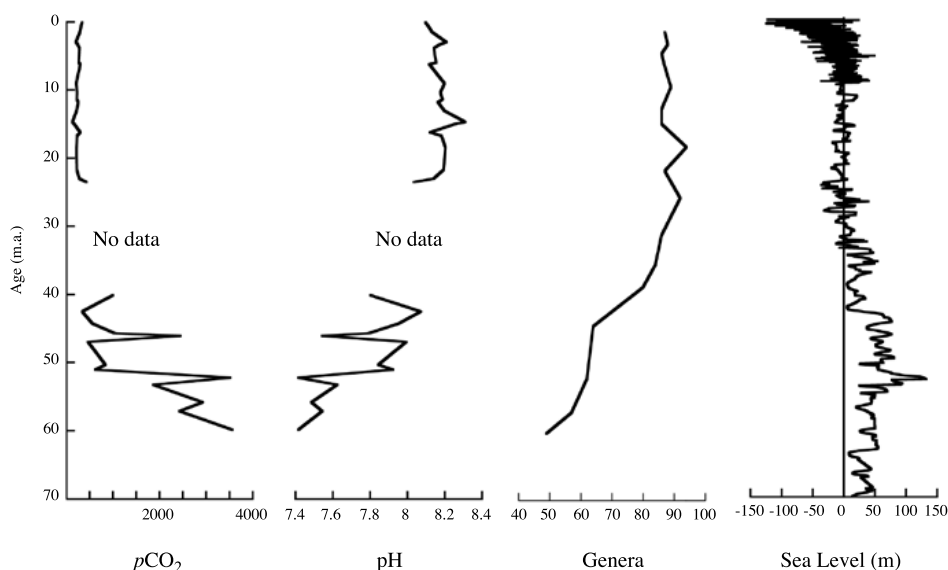
Today there is much concern over the degree to which ocean acidification associated with increased carbon dioxide (CO₂) will negatively impact biomineralisation in the sea³⁸. The fossil record is equivocal on this issue. For example, Palaeozoic reefs were dominated by calcitic corals so this part of the geological record is mute on the topic of the effects of ocean acidification on modern aragonitic corals. Late Cretaceous reefs were dominated by aragonitic corals until Mg/Ca ratios got low enough to favour the rudistid bivalves. The ‘Palaeocene lag’ in the recovery of reef ecosystems from the end-Cretaceous extinction is attributed to ‘calcite sea’ geochemistry¹²⁵. However, pH was lower in the Palaeocene as well (Figure 22.3). Following the Palaeocene, coral reefs diversified as ocean pH increased and atmospheric CO₂ decreased – see discussions below.

Figure 22.2 Secular trends in a variety of physical, chemical and biological attributes of the Earth system over the last 600 million years, Y-axis at same scale for all plots. From left to right: generic diversity of reef building corals^b; atmospheric CO₂ expressed as number of times higher than approximate present value of 300 parts per million by volume (RCO₂¹⁸); timing of flux in Mg/Ca concentration of seawater producing aragonite or calcite seas¹²⁵; global marine diversity (five largest mass extinctions indicated with crosses); timing of ice sheet advance/retreat during icehouse and greenhouse phases; global sea level, history of volcanic activity (biotic crises, climate, sea level and volcanic activity modified from Fischer¹¹)



b Paleobiology Database (2006) The data were downloaded from the Paleobiology Database on 24 May, 2006, using the group name 'marine invertebrate' and the following parameters: time intervals = Gradstein 7; Stages, region = Global, paleoenvironment = marine, order = Tabulata, Rugosa, Scleractinia

Figure 22.3 Secular variation of physical, chemical and biological attributes of the Earth system over the last 60 million years; $p\text{CO}_2$ and pH values from Pearson and Palmer¹⁰⁴; generic diversity of scleractinia from the Paleobiology Database^c; sea level data from Miller et al.⁸⁴



Sea level, sea surface temperature and global CO_2 levels

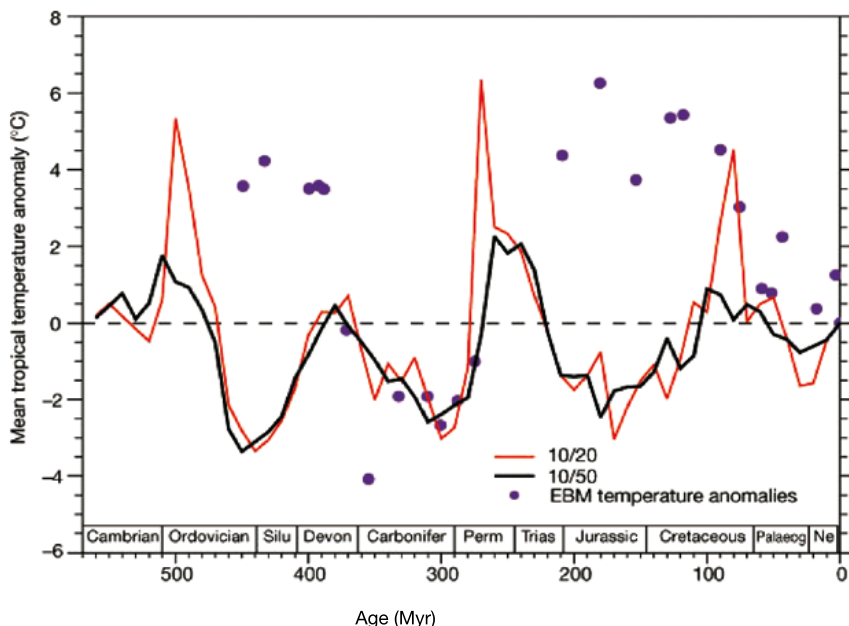
Fischer^{40,41} outlined a nested set of climate cycles apparent over the last 700 million years. These cycles, operating on timescales of 10^8 , 10^7 and $10^4/10^5$ years, were correlated with biotic crises observed in the fossil record of marine invertebrates. The longest cycle (defined by Fischer⁴⁰ to occur between 'Icehouse' and 'Greenhouse' intervals) was interpreted to be the result of changes in $p\text{CO}_2$ caused by variation in the Earth's mantle convection strength (and resulting sea-floor spreading rates). These refer to periods in which icesheets dominated the poles – the Icehouse, which we are currently in – and times when the poles were free from ice – the Greenhouse. These terms are not to be confused with glacial and interglacial periods, which can occur within these cycles. Greenhouse intervals occurred during the early-mid Palaeozoic and between Jurassic-Palaeogene time (Figure 22.2). They were characterised by high sea level (amplitudes are the subject of some controversy – recent work, eg Miller et al.⁸⁴, suggests that sea level in the Cretaceous was 100 ± 50 metres higher than today), rapid sea-floor spreading rates, elevated atmospheric CO_2 concentrations and elevated sea surface temperatures (5 to 9°C above present during Greenhouse II^{147,116}). In contrast, the Icehouse intervals bracketing the warmer periods were times of lower sea level, continental glaciation, lower concentrations of atmospheric CO_2 and lower temperatures (atmospheric temperatures 8 to 10°C below present during the glacial episodes of the present icehouse phase¹⁰⁶). Sea level variations accompanying transitions

c Paleobiology Database (2006) The data were downloaded from the Paleobiology Database on 24 May, 2006, using the group name 'marine invertebrate' and the following parameters: time intervals = Gradstein 7: Stages, region = Global, paleoenvironment = marine, order = Tabulata, Rugosa, Scleractinia

from Icehouse to Greenhouse intervals were up to 200 metres⁸⁴. Temperature fluctuations (examined as 10 million year or longer averages) in the tropics occurred at far greater magnitudes than have been observed today or projected into the future^{131,120} (Figure 22.4).

In a series of papers, Berner and colleagues^{16,17,18,20,19} quantified global atmospheric CO₂ levels over essentially the same time interval described above. Their model allowed only for long-term (again, 10 million year or longer averages) and hence short-term fluctuations were not delineated. Their results corroborated Fischer's^{40,41} earlier work. Very high levels (25 times that of today) of CO₂ were present during early Palaeozoic time (approximately 440 million years ago, during 'Calcite I', as defined above; Figure 22.2) followed by a large drop (ironically, to approximately modern levels: 306 parts per million by volume¹⁸) at 360 million years ago, near the end of Devonian time, most likely catalysed by the rise of vascular plants and their spread throughout terrestrial ecosystems^{2,111,35}. The resultant accelerated uptake of CO₂ by weathering of silicate rock as plants with deep root systems evolved was complemented by enhanced burial (and hence trapping of CO₂) of organic material in sediments. By 325 million years ago, the reduction of CO₂ was sufficient to plunge the earth into Icehouse II, which lasted 145 million years, into mid-Jurassic time. Greenhouse II persisted for approximately 150 million years, during its zenith in Late Cretaceous time (80 million years ago), CO₂ levels were five to six times higher than today^{18,103}. Beginning 33.5 million years ago, in Early Oligocene time, the earth began to enter the icehouse state (Icehouse III) that continues today.

Figure 22.4 Tropical sea surface temperature curve throughout the Phanerozoic derived from isotopic analyses (lines) and tropical surface palaeotemperature anomalies calculated by an energy-balance climate model (filled circles). 10/20 and 10/50 indicate running means at various temporal resolutions (eg 10/20 means step 10 million years, window 20 million year averaging) from Veizer et al.¹³¹



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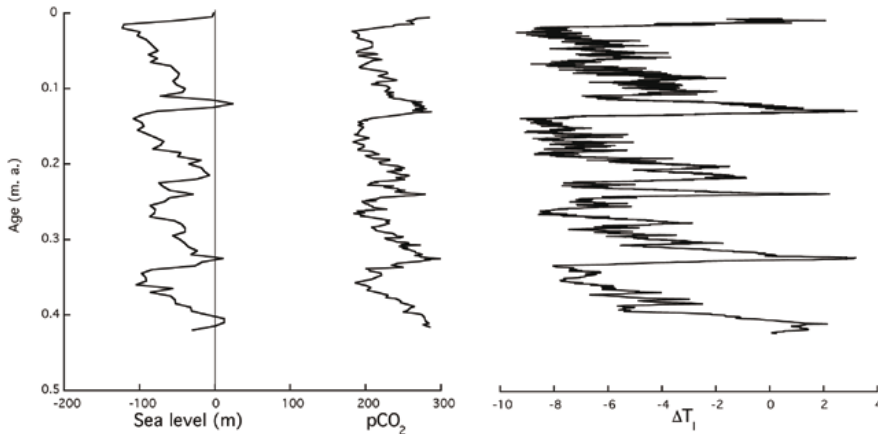
22.2.1.2 Quaternary rates and magnitudes of climate change

Milankovitch cycles

High-resolution climate proxies for the Quaternary, particularly the last 800,000 years, are derived primarily from deep-sea sediments and ice cores. These proxies indicate that, as the earth entered a full glacial period (a continuation of Icehouse III), growth and decay of ice sheets in the northern hemisphere were controlled by 10^4 - to 10^5 -year scale climate changes forced by natural cyclic changes in several parameters of Earth's orbit (so-called Milankovitch cycles⁸⁴). Global sea levels underwent at least 17 cycles of rise and fall during the last 500,000 years²⁷, with amplitudes of greater than 100 metres characterising glacial and interglacial stages. Average rates of sea level change between glacial and interglacial intervals approached 50 centimetres per century⁸⁴.

Variation in atmospheric CO_2 and global temperature in response to the waxing and waning of ice sheets also are recorded by climate proxies. Famously, the Vostok ice core spans greater than 400,000 years and records the atmospheric response to four complete glacial-interglacial cycles (Figure 22.5). At the onset of each warm interval, CO_2 increased by 8 to 10 parts per million by volume per thousand years, coincident with temperature increases of between 0.5 to 1.0°C per thousand years¹⁰⁶. During the latter half of this interval, rapid and dramatic changes in sea surface temperature have been calculated for the Western Mediterranean over the last 250,000 years, where rates of sea surface temperature increase have apparently exceeded 1.5°C per century⁸³. This record has now been extended, first with reports from the European Project for Ice Coring in Antarctica (EPICA) group of cycles back to 650 thousand years ago from a new ice core in Antarctica¹²², and then to 800,000 still showing Milankovitch cycles with temperature and CO_2 in lock step variation through the entire interval¹⁴⁵.

Figure 22.5 Climate and sea level fluctuations over Late Quaternary time. Sea level data from Miller *et al.*⁸⁴, CO_2 and temperature data from Petit *et al.*¹⁰⁶, temperature (ΔT_i) expressed as changes from the present temperature at the inversion (atmospheric) level



- d The cycles influence the amount of sun energy received by earth. They include obliquity (changes in the angle of earth's axis of rotation with respect to the sun); eccentricity (changes in the circularity of Earth's orbit around the sun); and precession of the equinoxes (changes in the position of the Earth in its orbit around the sun at the time of the equinox). The cycles are 41,000, 100,000, and 23,000 years, respectively.

Sub-orbital and abrupt climate change

Evidence from the last interglacial (approximately 128 to 118 thousand years ago) indicates substantial changes in sea level also occurred over much shorter intervals than could be produced by Milankovitch style forcing. For example, field evidence initially published for the Bahamas, indicates two episodes of reef building separated by a surface that clearly was exposed to the atmosphere. Dates obtained from corals preserved on either side of the exposure surface indicate that the fall and subsequent rise in sea level that produced the reef sequences occurred in as little as 1500 years and suggests rates of sea level change approaching 70 centimetres per century^{30,143}. Results of additional work in the Seychelles, Maldives and Western Australia^{54,137,138} suggests this also was a global sea level event.

A significant amount of new information has been gathered over the past several years that point to a large number of ‘abrupt climate change’ events during the more recent geologic past when most living marine communities originated and thrived. Abrupt climate change occurs when ‘the climate system is forced to cross some threshold, triggering a transition to a new state at a rate determined by the climate system itself and faster than the cause’⁸⁸. Recent palaeoclimatic studies indicate that regional temperature fluctuations of as much as 8 to 16°C occurred repeatedly in as little as a decade or less over the past 100 thousand years^{127,119}. One of the best known and studied of these events is called the ‘Younger Dryas’ event, so called because a cold-loving plant species’ pollen (*Dryas octopetala*, an arctic-alpine herb) reappeared during this interval. It had an abrupt beginning 12,800 years ago and an even more abrupt end 11,600 years ago. The intervening interval was characterised by cooler than normal temperatures, but the transition out of the cooling period resulted in a warming episode of 8°C in a decade.

During the last 10,000 years (Holocene time), rapid changes in climate, also on the scale of between 8 to 16°C, occurred repeatedly on decadal time scales^{119,4}. These changes were apparently forced by cyclic (1500-year) changes in solar activity/brightness²¹ and to date have been preserved by climate proxies in the northern hemisphere (eg Andresen et al.⁶ and Hu et al.⁶¹). Recently Mueller et al.⁸⁶ suggested that similar cycles of solar activity also operated during the last interglacial, 128 to 118 thousand years ago.

The best known of these types of short-term climatic cycles are the Dansgaard–Oeschger events and Heinrich events. Dansgaard–Oeschger events are a period of slow cooling followed by one of rapid warming. They have been detected by rapid shifts in isotopic composition in ice cores. Methane, regarded as an index of tropical wetland vegetation, also co-varies with the isotopic shifts. Heinrich events appear to be correlated with Dansgaard–Oeschger events and are characterised by the rapid break-up of northern hemisphere ice sheets that expand to a critical size, then break up along their oceanic margins. These events act as a switch to turn the Atlantic conveyor on and off, causing rapid climate changes in the north Atlantic region on the order of 5 to 10°C in a decade or less.

22.2.1.3 Summary

The long-term pattern of climate change preserved in the geologic record indicates substantial departures from that of human experience, especially magnitudes of temperature and CO₂ during deeper intervals of geological time. For example, temperature was up to 6°C higher in tropical Phanerozoic ecosystems than present day (Figure 22.4), similarly, CO₂ levels were up to 20 times

higher. Therefore, the *magnitude* of projected climate change is within the past history of metazoan, and even reef life, but the *rate of change* is unknown. This is due to the fact that the patterns in deeper time are not resolvable to scales relevant for present day changes because they are binned by 10 million year intervals, thus we don't yet know what the rate of change has been in deeper time when magnitudes exceeded present day and projected values.

Perhaps more relevant for modern managers are more recent patterns in temperature and CO₂ observed during the Quaternary, where both magnitudes and rates of change can be observed. Here we see that the magnitude and rate of temperature change are both greater in the Quaternary than projected for the next century by the Intergovernmental Panel on Climate Change (IPCC) (Table 22.1). Importantly, the highest rates of temperature increase during sub-orbital abrupt climate change events have not elevated Quaternary temperatures beyond those seen today. Projected temperature increases over the next century could elevate temperature near highest levels observed for the Quaternary. However, the rate of change in temperature will still be below the highest rates of change seen in the atmosphere during the initiation of each interglacial period within the last 400,000 years¹⁰⁶. In contrast, present day and projected magnitudes and rates of CO₂ rise now far exceed Quaternary levels (Table 22.1).

Table 22.1 Comparison of rates of change in temperature, CO₂ and sea level estimated for various intervals in the geologic past and those predicted for the next century. Where: kyr represents thousands of years, ppmv is parts per million by volume and m/century is metres per century

Geologic Interval	Age (kyr)	Temperature (°C/century)	CO ₂ (ppmv/century)	Sea level (m/century)	Reference
Pleistocene-Holocene	11.60 to 10.10	1.0	2.0	0.8	Severinghaus et al. ¹¹⁹ , Stocker ¹²⁷ , Miller et al. ⁸⁴
Pleistocene-Holocene	11.64 to 11.63	50 to 100*	N/A	N/A	Severinghaus et al. ¹¹⁹
Quaternary	156.35 to 129.70	0.042	0.34	0.52	Petit et al. ¹⁰⁶ , Miller et al. ⁸⁴
Quaternary	333.60 to 322.16	0.12	3.4	0.56	Petit et al. ¹⁰⁶ , Miller et al. ⁸⁴
Palaeocene-Eocene	55,000 to 54,925	0.007	0.2	0.06	Zachos et al. ¹⁴⁷ , Miller et al. ⁸⁴
Next Century	N/A	1.2 to 5.8	111 to 732	0.07 to 0.86	IPCC ⁶⁴

* Represents estimate for a 'decadal step' associated with the end of the Younger Dryas Interval



22.2.2 Sensitivity

22.2.2.1 Phanerozoic reef response

Reef systems have a geologic history extending back 2.5 thousand million years or 2.5 Ga. Then, microbial stromatolites built wave-resistant structures soon after tectonic processes produced widespread shallow marine shelf environments⁸⁹. Reef systems comprising corals extend to at least 450 million years ago⁵⁸ and most likely earlier¹¹⁵. Over geological timescales since that time, reef coral communities have been durable in the face of global biotic crises, reappearing after each of the 'big five' mass extinction events¹¹⁰ and numerous smaller mass extinction events. However, recovery intervals ranged from four million years (following the end-Triassic event^{132,136} to over 100 million years (following the collapse of the mid-Palaeozoic reef ecosystems beginning near the end of Devonian time⁸⁹). Although reef crises are correlated with mass extinction events, Flügel and Kiessling⁴⁴ have demonstrated that the magnitude of mass extinctions and reef crises (the former measured as declines in biodiversity, the latter as declines in carbonate production) are rarely equivalent, suggesting that they are not always causally related.

Early to mid-Palaeozoic coral reef ecosystems fall into 'Calcite I' of Sandberg¹¹⁴, and are dominated by calcitic rugose, tabulate and heliolitid corals (as well as calcitic stromatoporoid sponges). The collapse of the Devonian coral reef ecosystem resulted in a loss of framework-building taxa and was followed by a transition to 'Aragonite II' in mid-Mississippian time¹¹⁴. Although coral components of reef ecosystems are unimportant during the latter half of the Palaeozoic, algae secreting high-magnesium calcite skeletons and aragonitic phylloid algae became dominant constituents of late-Palaeozoic reef ecosystems^{146,43}.

'Aragonite II' persisted through the Permo-Triassic extinction event; when reef building resumed in mid-Triassic time, a community of high-magnesium and aragonitic organisms (notably sponges and red algae) were responsible^{45,118}. Scleractinian or 'stony' corals, which build aragonite skeletons, join these communities in Late Triassic time^{126,15} and, following the end-Triassic extinction, dominate global reef systems until the mid-Cretaceous shift from aragonite to calcite seas^{124,76}. By Late Cretaceous time, calcitic rudistid bivalves began to supplant scleractinian corals as dominant reef builders^{117,69}. Stanley and Hardie¹²⁵ suggest that the replacement of scleractinians by rudists was a consequence of the decline of aragonitic corals resulting from a pronounced decrease in the magnesium/calcium ratio of sea water by Late Cretaceous time.

The timing of recovery of the coral reef ecosystem from the terminal Cretaceous extinction event is the subject of some controversy. Many researchers have suggested that reefs did not attain Cretaceous levels of geographic extent and complexity until Oligocene-Miocene time: the beginning of 'Aragonite III' (Figure 22.2) (eg Frost⁴⁸, James⁶⁸, Sheehan¹²¹, Fagerstrom³⁷, Bryan²⁴, Hallock⁵⁵, Stanley and Hardie¹²⁵). More recently however, Baceta et al.⁸ suggest that this impression may largely be the result of preservation bias, and present an analysis of an extensive early Palaeogene section to demonstrate a rapid (two million years) recovery of coral-dominated reef systems. Moreover, Kiessling and Baron-Szabo⁷³ show that extinction rates of scleractinian corals across the Cretaceous/Palaeogene boundary were only moderate in comparison with other invertebrates.

What is clear is that luxuriant and widespread reef growth is observed during the Oligocene Epoch of the Palaeogene Period^{47,48}, even after global climates had cooled substantially¹⁴⁴. This interval coincides with the onset of 'Aragonite III' and the establishment of Mg/Ca ratios sufficiently high to allow aragonitic reefs to flourish once again.

Reefs tend to disappear significantly earlier than other taxa at terminal extinction events. For example, Cretaceous reefs vanished 0.7 to 1.5 million years before the end-Cretaceous extinction⁷⁰. This general pattern holds also for the reduction and collapse of early and middle Palaeozoic reefs, which generally occurred 0.5 to 1.0 million years earlier than the accepted extinction boundaries for Early Cambrian, Late Ordovician and Late Devonian events³¹. This suggests that, regardless of the cause of extinction, reef ecosystems might be more sensitive indicators of environmental perturbation than are other taxa.

Kiessling⁷¹ presented a synthesis of the palaeolatitudinal distribution of 2910 Phanerozoic (pre-Quaternary) reef (corals and other important calcified constituents) sites compiled from the literature and compared it to a variety of palaeoclimatic curves that included temperature and atmospheric CO₂^{46,16,131}. Neither the total latitudinal range of reefs nor the width of the tropical reef zone was significantly correlated with palaeoclimate inferred from the subsidiary data⁷¹. Relevant for living coral reefs, Kiessling⁷¹ observed that fluctuations in the width of the tropical reef zone were in phase with climatic variations only during Cenozoic time.

The influence of seawater chemistry on skeletal mineralogy appears to be particularly strong for morphologically simple taxa that exert relatively weak control over their own calcification – including reef-building corals. Hence, the Mg/Ca ratio and saturation state of carbonate in sea water have been first-order controls over the success of individual reef-building taxa, resulting in a remarkable correspondence between their mineralogy and that of inorganic carbonates over geologic time. Ries et al.¹¹² provide experimental evidence that changes in seawater chemistry may result in the precipitation of biogenic calcite in scleractinian corals that exclusively precipitate aragonite skeletons. Modern corals grown in aquaria full of 'Cretaceous' seawater with reduced Mg/Ca ratios compared with present day also grew more slowly. Ries et al.¹¹² relate the mid-Cretaceous decline and Oligocene resurgence of corals as reef builders to the variation in seawater Mg/Ca ratios. Future experimental work on changing seawater chemistry and its effects on coral growth over longer time intervals will be a welcome addition to understanding the effects of climate change and ocean acidification on coral reefs. Fine and Tchernov³⁹ showed that scleractinian corals grown in experimental acidified conditions lost their skeletons, but were able to sustain basic life functions, including reproductive ability, in a sea anemone-like form. They resumed skeleton-building when reintroduced to normal marine conditions. They concluded that 'physiological refugia' allow corals to alternate between non-fossilising soft body forms and fossilising skeletal forms in response to changes in ocean chemistry.

In summary, coral-dominated reef systems recovered after past climatic instability imparted as the Earth passed between one stable climatic state and the other. It is clear that the acme of reef development, both in geographic extent and coral diversity (Figure 22.2), occurred during past Greenhouse intervals. Prior to the mid-Palaeozoic (Late Devonian) collapse of the reef system, equatorial reef and inter-reef carbonate platforms covered an estimated 10 times the areal extent witnessed today³¹. In contrast, the rise of the modern reef system beginning in mid-Palaeogene time occurred in tandem with falling levels of atmospheric CO₂, increasing Mg/Ca, increasing alkalinity of the world's oceans and global cooling (Figure 22.3). Hence, aragonite-secreting corals, living in a chemical environment that fosters

precipitation of aragonite, build reefs today. This combination of climatic and geochemical factors was not present during intervals in the geological past that witnessed widespread reef development. Therefore, it would be imprudent to cite widespread reef development during past Greenhouse intervals as evidence that the modern reef system will likely benefit from climate change.

22.2.2.2 Quaternary reef response

The Quaternary fossil record of reef coral communities is an ideal database for assessing the vulnerability of the modern reef system to climate change. First, reef coral communities preserved in Quaternary strata are taxonomically congruent with modern reef coral communities^{65,92}. Second, Quaternary reef coral communities flourished during an interval of rapid and dramatic climate change for which highly precise climate data are available (Figure 22.5). Third, during the last interglacial, sea level was two to six metres higher²⁹, with consequent exposure of a two to six metre terrace throughout the tropics that preserves coral reefs. Finally, Quaternary fossil reef communities are remarkably well preserved⁵⁰ allowing for a great number of coral taxa to be identified with a degree of certainty that compares closely with modern taxa^{95,96,99,97}.

Recent studies have examined reef coral community dynamics over geologic time scales (Late Pleistocene and Holocene time) and extended spatial scales (10 to 1000's km) and applied the results to further our understanding of processes affecting the community structure of modern coral reefs (reviewed in Pandolfi⁹⁴ and Pandolfi and Jackson⁹⁸). For coral reefs, palaeoecology provides a unique tool for placing perturbations affecting modern reefs into a temporal context that exceeds the scope of traditional ecological studies^{93,63,100}. An additional body of recent work has compared the community structure of Pleistocene reef corals to that of modern reef coral communities to assess whether a precedent exists for the ongoing collapse of modern reef systems^{7,53} as well as the magnitude^{66,67} and mechanism¹⁰⁰ of the collapse. On a global scale, coral species underwent dramatic changes in distribution and abundance during Quaternary glacial-interglacial cycles that caused sea level to repeatedly flood and drain from continental shelves and oceanic islands¹⁰⁸.

The higher resolution provided by the Quaternary (the last 2.6 million years) fossil record of coral reefs provides an opportunity to dissect the broad patterns of response observed over an eon of geologic time. Moreover, modern coral communities are derived largely from species that survived biotic turnover in Plio-Pleistocene time^{132,25}. Hence, a review of the response of these communities to the rapid and dramatic fluctuations in temperature, sea level, and atmospheric CO₂ that characterise the Late Quaternary is especially appropriate for an assessment of the vulnerability of the modern reef system to climate change.

The Great Barrier Reef

The history of the Great Barrier Reef (GBR) spans multiple episodes of global environmental change, yet it is a relatively 'young' geological structure that did not respond to favourable environmental conditions early on. In fact, the central Queensland continental shelf has enjoyed warm tropical waters that could well have supported coral reef growth for the past 15 million years³³. However, it is now generally recognised that the initiation of the GBR did not occur until approximately 600 thousand years ago, and the GBR reefs as we know them probably didn't occur until around 365 to 452 thousand years ago³⁴. This is coincident with Marine Isotope Stage 11, perhaps the warmest interglacial of the past 450 thousand years⁶⁰, and one with climatic conditions most similar to those

we are now experiencing⁷⁷. Larcombe and Carter⁷⁵ believe that the ‘switching-on’ of the GBR was not only related to the ‘mid-Pleistocene transition’ from 41 to 100 thousand year-long climatic cycles¹⁴, but also to the development during Marine Isotope Stage 11 of a marked high stand that enabled sustenance of both a cyclone corridor and a reef tract along a relatively wide and deeper water continental shelf.

Webster and Davies¹³⁴ showed remarkable consistency in community composition throughout many intervals of Pleistocene reef development on the GBR at Milankovitch time scales. Recent cores drilled through Ribbon Reef 5 have shown that the GBR has been able to re-establish itself repeatedly despite major environmental fluctuations in sea level, temperature and CO₂ over the past several hundred thousand years¹³⁴. Moreover, Webster and Davies¹³⁴ showed that the reefs have maintained a similar coral and algal species composition during their repeated formation. Species abundance data were derived from 55 coral species from 20 genera and coralline algal associations were derived from an analysis by Braga and Aguirre²³.

Growth of the GBR’s fringing and nearshore reefs during the past 10 thousand years (the Holocene) has been upon Pleistocene topographic highs¹²³. Holocene fringing reef growth on the GBR varies naturally through time and appears to be episodic, responding closely to sea level and climate change¹²³. The most significant period of active reef growth occurred between 7500 and 5500 years before present as the post-glacial marine transgression (sea level rise) progressed. Smithers et al.¹²³ attribute the turn-off of these reefs at the end of this period to the exhaustion of available accommodation space (the water depth of the shallowest growing reef) over suitable substrates, stresses associated with sea level stabilisation and slight fall near the end of this time, and climate changes associated with changes in the intensity and frequency of El Niño-Southern Oscillation conditions. They also noted other periods of moribundity since the mid-Holocene that are related to the filling of accommodation space, reduced flushing since the optimal Holocene high-energy window (7500 to 5500 years before present) and reduced calcification and increased disturbance associated with climate changes. These moribund reefs were characterised by healthy but non reef-building coral communities. The authors note that many living fringing nearshore coral reefs are built upon reef structures that were constructed in the distant past. The main point from these findings is that interruptions in reef growth, even climatically induced, are part and parcel of the Holocene nearshore record, but the living biophysical structure of the coral reef remained in the face of episodic moribundity, much of which can be correlated with climatic changes.

Indo-Pacific coral reefs

Like the GBR, Indo-Pacific reefs have flourished throughout several Milankovitch cycles during the past several hundred thousand years. For example in Papua New Guinea, vibrant interglacial reefs preserved in uplifted terraces along the northern coastline of the Huon Peninsula preserve fossil reefs over at least the past 340 thousand years²⁸. These Pleistocene reef coral assemblages show pronounced constancy in taxonomic composition and species diversity between 125 and 30 thousand years⁹². Differences in reef coral community composition during successive high stands of sea level were greater among sites of the same age than among reefs of different ages, even though global changes in sea level, atmospheric CO₂ concentration, tropical benthic habitat area and temperature varied at each high sea level stand⁹³. Thus, local environmental variation associated with runoff from

the land had greater influence on reef coral community composition than variation in global climate and sea level. There is also evidence that ecologically equivalent reefs were built successively during subsequent glacial intervals (sea level low stands) in Papua New Guinea¹³⁵.

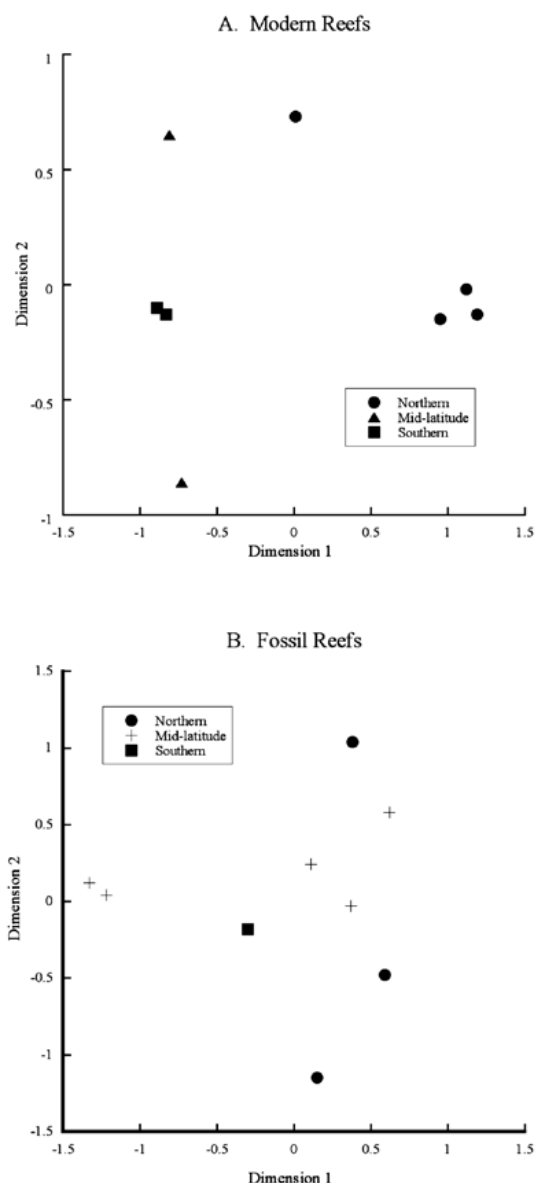
Western Australia

Present global climate change is resulting in noticeable range expansions of living corals^{82,130,109}. Recent work^{51,52} in coastal Western Australia has provided preliminary data on how such range movements might affect the long-term ecological dynamics of coral reef habitats. Well-preserved exposures of Late Pleistocene coral reefs are accessible at several localities over a distance of approximately 12 degrees of latitude that today encompasses the boundary between two biogeographic provinces (Figure 22.6). Comparison of reef coral community composition between adjacent modern and fossil reefs along this environmental gradient revealed that coral taxa expanded their latitudinal ranges during Late Pleistocene time compared to today. The two primary consequences of the range expansions were: i) a reduction of the latitudinal gradient in community composition relative to modern reefs (Figure 22.7), and ii) a resultant lower coral diversity within the latitudinal range.

Figure 22.6 Modern and Pleistocene reef localities from Western Australia compared by Greenstein and Pandolfi^{51,52}. Modern localities in *italics*, except for the Houtman-Abrolhos and Rottneest Islands, which expose both modern and fossil reefs. Additional fossil localities include Cape Range, Lake Macleod-Cape Cuvier (L. M. – C. C.) and Port Denison. Province designations after Wilson and Gillett¹⁴²



Figure 22.7 Results of two-dimensional non-metric multidimensional scaling of Bray-Curtis dissimilarity values calculated from presence-absence data obtained from modern and Pleistocene reef coral assemblages of Western Australia. A) Modern reefs show a clear distinction, along Dimension 1, between the high-diversity northern reefs of Ningaloo and lower diversity southern reefs of Rottnest Island. A significant ($R^2=0.81$; $p < 0.0001$) correlation exists between Dimension 1 and latitude. Stress for the analysis was < 0.001 ; B) Pleistocene reef assemblages exhibit a significant, though not as strong, ($R^2 = 0.66$; $p < 0.01$) correlation between Dimension 1 and latitude suggesting that the past distinction of reef coral communities between Cape Range and Rottnest Island was apparently less developed than it is today. Stress for the analysis was 0.09



A major implication of the patterns observed in Western Australia for the GBR is that increased range shifts of modern corals in response to climate change in the near future could potentially lower regional coral diversity in a similar fashion. The role of biodiversity in enhancing ecological stability has been demonstrated on small spatial and temporal scales^{79,87,81}. For coral reefs, the diversity-stability relationship apparently scales up to regional spatial scales¹² and geologic time scales⁷². Hence, mitigation of current threats to coral reef diversity and function becomes especially critical.

The last glacial maximum

The last glacial maximum, dated to about 18 thousand years ago was a time when sea levels dropped to approximately 120 metres below present day levels. Kleypas⁷⁴ estimated the amount of area available during such a drop in sea level for the Caribbean Sea and compared it to modern potential sites for reef growth. She found a greater than 90 percent drop in areas for potential reef growth during the last glacial maximum as compared with the present high sea level stand. Yet coral reef growth since then has been shown to accrete at some of the highest rates observed in coral reef settings. This is shown in the record of reef development from both Barbados and the Huon Peninsula²⁹. This interval of reef growth appears not to have been unduly affected by initial starting conditions under which the areal extent of suitable habitat was an order of magnitude less than present.

Response to sub-orbital climate events

Perhaps the best-known sub-orbital climate event is the Younger Dryas event occurring 11 to 10 thousand years ago. In cores from both Barbados and Huon Peninsula, and in raised reef terraces from Huon Peninsula (Pandolfi unpublished data), rates of coral reef growth during the event itself were indistinguishable from growth before and after the event. This does not mean that reef growth was unaffected by the event since short-term interruptions in reef growth may be difficult to identify in ancient reef deposits. However, the Holocene raised reef terrace from Huon Peninsula, Papua New Guinea, preserves mass mortality events of reef corals mainly from volcanic episodes¹⁰² and the resolution of these intervals is approximately 200 years.

22.2.3 Adaptive capacity

Many marine species exhibit a genetic legacy of latitudinal range shifts, local extinctions and expansions, and the marked population fluctuations caused by past climatic variation⁵⁷. Based on this past history, can we expect that regional and global-scale disruption to coral reefs generally, and to the GBR in particular, due to climate change will accelerate markedly in coming decades? Already, relative abundances of corals and of other organisms are changing rapidly in response to the filtering effect of differential mortality (from bleaching and other, more local, human impacts), and differences in rates of recovery of species from recurrent mortality events^{9,78,62,90}. Furthermore, many, mainly terrestrial, organisms are already showing signs of evolutionary change in response to climate-induced environmental variation²². The degree to which this will hold in coral reefs is subject to intense debate, but the near and distant geological record preserves clear evidence that coral reefs have re-established after previous events. This indicates their ability to either adapt to changes, or exploit refugia in less affected areas, so that when optimal conditions returned, they again spread throughout their range.

Our results from Western Australia indicate that reef corals are able to expand their latitudinal ranges in response to climate change. Work by Pandolfi⁹² indicates that refugia also have played a role in the re-establishment of reefs during intervals of climate change during the last 100 thousand years. Refugia likely were important to the survival of molluscan faunas during this same interval^{128,129}.

22.2.4 Vulnerability and thresholds

The vulnerability of the GBR to projected global climate change cannot be considered without an understanding of both the history of reef development and the history of impacts that have led to habitat degradation. The diversity, frequency and scale of human impacts on coral reefs are increasing to the extent that reefs are threatened globally¹⁴¹. Until recently, the direct and indirect effects of overfishing and pollution from agriculture and land development have been the major drivers of massive and accelerating decreases in abundance of coral reef species^{85,67,1,49,63,100}. These human impacts and the increased fragmentation of coral reef habitat are unprecedented and have the possibility to undermine reef resilience¹³, raising the likelihood that modern coral reefs might be much more susceptible to current and future climate-change than is suggested by their geologic history^{63,13}.

Recent work has sought to understand human impacts by developing time-series data archives that can be used to evaluate trends in the global decline of coral reefs since the arrival of humans. The approach has been to use a number of different kinds of data during several periods to examine the recent past history and present condition of coral reefs to provide a natural baseline for community ecology and coral growth rates. Archaeological sites provide insight into the relationship between the development of civilisation and its evolving impact on coastal marine resources. Historical records such as those found in ships logs, and publications of early naturalists and European colonialists provide a moving window of the natural history and inferred ecology of many coral reef inhabitants. Fisheries records and modern ecological surveys can be used in association with remote sensing data (going back the last 20 or 30 years) to provide a detailed picture of changing environments and biodiversity as human population and consumption, as well as economic globalisation, have accelerated during the past several decades. To document changing physical environments, coring of reef corals provides a proxy for sea surface temperature, rainfall, and river discharge⁸⁰ from the geological past to the present. Taken together, these databases provide a holistic view of changing environments and ecology on coral reefs that includes the onset of human disturbances and against which the acquisition of present day data can be evaluated.

Recent findings from sites distributed throughout the tropical world point to the immense importance of understanding historical events when attempting to tease out factors that have or may influence present coral reef biodiversity¹⁰⁰. At 14 sites worldwide (including the outer and inner GBR and Torres Straits) there was no increase in the acceleration of reef megafauna decline during the past century when disease and climate change appear to have intensified, rather, early and effective overfishing appears to have been the major culprit in reef decline¹⁰⁰. A recent paper explored the policy implications of the historical ecological work and urged US government officials to adopt the large percentage of no-take areas for their reefs as Australia has done¹⁰¹. The main conclusions from the work were: i) overfishing is by far the earliest and most influential human impact on coral reef ecosystems, ii) degradation of coral reefs proceeded from the earliest human interactions and was independent of population growth, and iii) if the trajectories of change on coral reefs are not reversed



the current rate of decline in reef ecosystems will result in their extirpation independent of what happens to Earth's climate. Correlation of reef decline with specific human and environmental impacts over time provides an insight into the processes that are most important in local reef settings. When these processes are uncovered, specific steps can be taken to ameliorate or reverse the decline.

22.2.5 Threats to resilience

The magnitude and frequency of documented incidences of abrupt climate change during the recent past history of living coral reefs (less than one million years) has been substantial, yet nowhere have the effects of this change been rigorously studied. This is in part due to the juxtaposition of geological processes operating over geological time scales onto ecological processes operating over much shorter intervals. The geological record does tell us that IPCC predictions for 21st Century climate change for sea level and sea surface temperature (SST) fall within the rates and magnitudes experienced in the recent geological past of living coral reef assemblages, but for CO₂ they do not. The recent past history of modern coral reefs shows no slowing of reef growth through extreme SST and sea level events (Table 22.1). Ecologists and managers concerned about the vulnerability of reefs to projected rapid climate change must acknowledge the ability of coral reefs to either survive or quickly recover from extreme SST and sea level episodes. Study of the mechanisms through which reef survival or replenishment occurred over these intervals should allow for a better understanding of threats from climate to coral reefs over the next century. Similarly, the modern reef's ability to cope with unprecedented changes in the rates and magnitudes of CO₂ must also be seriously considered.

It is clear to us that climate change is coupled with multiple anthropogenic effects that are likely to threaten the global reef system. For the GBR, areas that are less influenced by humans such as the outer GBR are the least vulnerable while inner GBR areas that have suffered more from coastal influences would be more likely to suffer. Ultimately, this is an optimistic assessment since mitigation of local and regional sources of disturbance along the GBR are more easily achieved than mitigating increasing atmospheric concentrations of greenhouse gases.

As a paradox when considered in the context of past abrupt climate change and the apparent lack of permanent deleterious ecological effects, it is clear that marine ecosystems in general, and coral reefs in particular have been able to either survive from or quickly reconstitute after repeated extremes in climate. The mechanisms by which such resilience occurs need to be meted out, along with how that resilience is affected by the anthropogenic stress already imposed on living reefs prior to and concurrent with climate change. What are the mechanisms by which such resilience to climate change might have occurred in the past, and how will this resilience be affected by the anthropogenic stress already imposed on living reefs prior to and concurrent with climate change? For example, how does response to environmental change differ between exposure of pristine reefs to the abrupt climate change in the past versus overfished or polluted reefs today¹⁰⁰? The El Niño event of 1998 was instructive in that pristine reefs suffered bleaching equally to degraded reefs¹⁴⁰. However, recovery times were markedly different¹⁰⁵. What do past abrupt climate change events teach us about the ecological consequences of future climate change on coral reefs? Put another way: what, if anything, is fundamentally different about the global reef ecosystem today compared to the systems that either survived during or re-established after multiple climatic changes? The answer suggested by the historical and geological record is the presence of increasing anthropogenic disturbances.

22.3 Summary and recommendations

22.3.1 Major vulnerabilities to climate change

One of the major vulnerabilities to climate change for the GBR is abrupt climate change. Most ecologists attempting to come to grips with the implications of climate change to their ecosystems are still envisioning climate change as gradual change associated with increased greenhouse gas emissions, albeit much faster than perceived rates of past change. Ecologists may be dramatically underestimating the magnitude, speed and extent of past climate change^{3,4,5} (Table 22.1). It is now becoming increasingly clear that sub-orbital and abrupt climate change events are part of natural climatic cycles. We need to better understand what the relationship is between the triggers of these events and rising climate change and what the effects will be on coral reef communities. Another key climate component is the dramatic rate of increase in CO₂ levels. Though levels of CO₂ have been substantially higher in the geological past, the ability for living corals and associated reef taxa to cope with present dramatic rates of change is unknown.

22.3.2 Potential management responses

Our recommendations concerning the vulnerability of coral reef communities of the GBR to projected change in climate over the next century are based on three pillars that summarise the results presented herein: i) The rates and magnitude of sea level and temperature changes over the next century are no greater than those experienced by living coral reefs throughout the past several hundred thousand years, but the magnitude and rates of CO₂ rise are much higher than over the same interval; ii) the presence of Pleistocene fossil reefs at localities extending up to 500 km south of the limit to their modern counterparts in Western Australia suggest that, given suitable substrates and water clarity, coral reefs can expand their latitudinal range during episodes of heightened water temperatures (see also southern reef occurrences along eastern Australia¹⁰⁷); and iii) coral reefs have been substantially impacted by human activities that appear to have accelerated in their intensity. Thus, dramatic changes in the magnitude and rate of change in climate variables coincide with impacted reefs that are heavily degraded by human activities.

Recommendations

Our first recommendation is to immediately reduce human impacts on the GBR that are unrelated to climate change. Planned response to projected climate change on reefs should aim to increase the ability of coral to respond positively. We know that it is possible for 'natural' coral reefs to withstand severe changes in climate over short periods, so this will best be accomplished by reversing and mending reef degradation that has already occurred. This view stems not from denying the potential for large-scale mortality as a result of climate change; but is based on the response of reef growth through similar past intervals as evidence that the ecosystem has the potential to be resilient to climate change. Reefs have repeatedly assembled after multiple periods of moribundity, even on the GBR¹²³. Therefore, even though present day coral distributions might reflect the upper thermal tolerances of corals⁴², the larger pattern suggests that even large-scale mortality may not result in the permanent demise of coral reefs worldwide over a *geological* timescale. One has to entertain the possibility that a more global view of reef distribution provides insurance against reef extinction when heightened temperatures and CO₂ occur during climate change.

One scenario that might have resulted in continuity of reef development over abrupt climate change events occurred during the last interglacial period. Extension of coral reefs during the last interglacial resulted in the occurrence of vibrant, diverse coral reefs as far south as Rottneest Island in Western Australia and Evan's Head¹⁰⁷ in New South Wales. Let's imagine that past spikes in temperature resulted in a significant increase in coral bleaching events and greater than 90 percent coral mortality in the previously defined reef areas at low latitudes. New areas south of the original extension of coral reefs may have acted as relict populations seeding reefs further north, leading to subsequent sustained recovery of northern Australian reef populations. Southern populations have a precedent for re-seeding northern reefs on the GBR during glacially-induced sea level rises (since deeper southern GBR reefs probably supported reef growth sooner than the shallower shelf where northern GBR reefs reside), for example from the last glacial maximum 18 to around six thousand years ago. Clearly, extension of GBR corals south of their present ranges will depend on a myriad of factors, including substrate availability and ocean acidity. Regardless of the efficacy of this scenario, the important point is that past reefs, even on local spatial scales, have survived or quickly recovered from past climate fluctuations. Again, the important differences in the modern setting are anthropogenic degradation and heightened rates and magnitudes of CO₂.

Our second recommendation is to re-focus management away from maintenance of the status quo ('our GBR – let's keep it great') to active restoration of reef resilience ('our GBR – let's get it back'). The best way of ensuring the successful transition of GBR reefs through abrupt or gradual climate change is to restore the ecosystem to good health. It is apparent that this is not presently the case for the GBR^{100,101,13,36}. Therefore, management actions cannot only protect areas of the reef from further degradation. Instead, management must now take proactive steps that recover losses and reverse the trajectory of decline¹⁰¹. Efforts toward large-scale and whole-sale restoration of both herbivore populations and nearshore water quality represent the most immediate challenges.

We recommend positive actions that adhere to a 'no-regrets' policy and provide benefits regardless of the magnitude, rate or degree of future climate change⁸⁸. Both scientific and political activities should be geared toward enhancing the ability of the GBR to weather the coming climate storm; if no such storm arises, then such activities will still have been favourable to the intelligent management of one of Australia's leading tourist attractions and, more importantly, one of its national treasures. We can think of no better 'no-regrets' policy than reversing the trajectory of decline of the GBR, restoring the majestic trophic structure that Captain Cook took in when first plying the emerald seas of this brave new world.

22.3.3 Summary

Some of the physical changes that are projected to occur in the coming century⁶⁴ have occurred repeatedly throughout both the past two million years of the Quaternary period and in the more distant past, while others have not. Reef coral communities in the distant past rebounded from decimation resulting from climatic events that affected the global marine biota. Recovery intervals varied from four to 100 million years, during which time framework building organisms were largely absent from reef ecosystems. More recently, Quaternary coral reef development either proceeded undeterred throughout climatic changes or recovered so quickly as to leave no record of their demise. The major difference between past reefs and those confronting climate change in the next

century is that today's reefs have been preconditioned by human impacts such that the frequency of disturbance might have decreased their resilience to perturbations⁶³. Thus, the GBR is vulnerable to global climate change not only because of the physical changes in environmental conditions, but also because these changes will be brought upon an already stressed ecosystem.

22.3.4 Further research

Consideration of acclimation and adaptation of coral reefs in the context of new advances in climate research and anthropogenic stress provides a significant step forward in the inter-disciplinary synthesis and prediction of coral reef response to climate change. For their part, coral reef ecologists and physiologists are engaged in a lively debate over how climate change might impinge on the survival and growth of coral reefs. The debate encompasses views ranging from extirpation⁵⁹, to change but not extirpation⁶³, to intact survival^{26,10,11,113}. Nowhere in the debate is there a consideration of 'abrupt climate change' in the geological past (which reefs have either survived or quickly replenished from) or future (which will occur to anthropogenically stressed reefs¹⁰⁰). Current debates on coral/symbiont acclimation or adaptation need placement in the context of historical response of natural reefs to 'abrupt climate change' vs. future response on modern, anthropogenically stressed reefs.

One of the great challenges is to generate information on the role of habitat degradation and loss of biodiversity on the resilience of GBR communities. In the face of imminent climate change there will be cries from every field of inquiry for immediate research needs. An immediate concern is an understanding of how to foster resilience of already multiple-stressed coral reef communities (by anthropogenically-induced sources of mortality and habitat degradation) under impending predicted climate change. In other words, we need a better understanding of how resilience can be maintained and improved in impacted coral reefs. For example, the diversity-stability relationship has been established at both ends of the spatio-temporal spectrum (short observation intervals and experimental scales to millions of years and global scales). Understanding this relationship at intermediate scales – the range of long-term ecosystem management – will facilitate our ability to foster resilience. An understanding of improving resilience is probably the best defence we can have over a highly variable and potentially unpredictable future.

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